DECREASE IN SEXUAL DIMORPHISM OF BAR-EYE DROSOPHILA DURING THE COURSE OF SELECTION FOR LOW AND HIGH FACET NUMBER[1]

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IN the bar-eye race of *Drosophila* the mean eye facet number of the males is higher than that of the females, though there is an overlapping in range as shown in Table I. In the unselected white bar stock used as the starting point of a series of selection experiments this difference amounted to 6.12 factorial units, a factorial unit being one that produces a ten per cent. change in facet number. If this value were fairly constant it would be possible in treating the selection data statistically to reduce the facet values of the two sexes to a common basis in much the same way that Galton obtained a mid-parental value in his studies of the inheritance of human stature. Such a procedure was followed by Zeleny and Mattoon (1915)[2] in their paper on selection in red bar-eye. In attempting to apply the same method to the white bar series it was discovered that the difference between the two sexes is not constant but decreases during the course of selection. It is therefore not practicable to apply a constant coefficient for the reduction of the value of one sex to that of the other.

The selection experiment in question started with a white bar stock which had been obtained by crossing white full-eye to bar-eye. Single pair, brother and sister, matings were adhered to with a few breaks due to sterility. In the low line the lowest available virgin female

[1] Contribution from the Zoological Laboratory of the University of Illinois, No. 187.

[2] Zeleny, C., and Mattoon, E. W., 1915, "The Effect of Selection upon the 'Bar Eye' Mutant of *Drosophila*," *J. Exp. Zool.*, 19: 515–529.

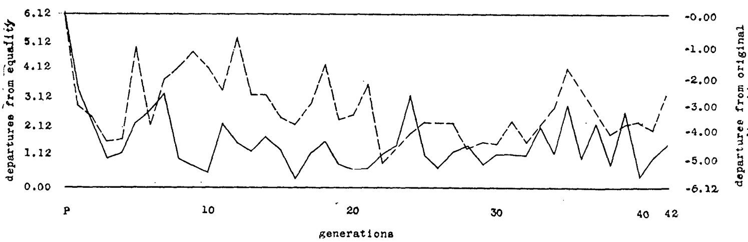

FIG. 1. Sexual dimorphism in each of the selection generations. Direct matings only. The difference between males and females is expressed in factorial units, a factor of unit value being one capable of producing a ten per cent. change in facet number. In the unselected population this difference amounts to 6.12 units and in the figure such a value is represented by the upper horizontal line. A zero difference between the sexes is represented by the lower horizontal line. The scale of departure from equality is shown at the left hand and the scale of departure from the original value in the unselected population at the right hand.

was mated to her lowest available brother in each generation with duplicate matings to insure the continuation of the line. In the same way in the high line the female with the highest facet count was mated to her highest brother.

The data as given in the present paper are grouped under two heads. In Table II and Fig. 1 are included only those individuals in the direct line. In Table III and Fig. 2 there are included, in addition, the sib matings in each generation. The general results obtained from the two groupings are alike, but the data based on all the matings give a smoother curve because of the larger numbers of individuals involved.

Table I shows the distribution of frequencies of factorial values for eye facet number in the unselected population of white bar, number 127, which served as the

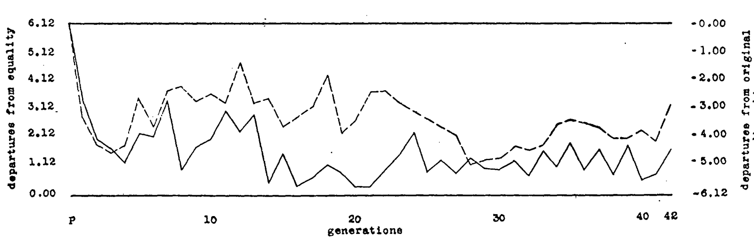

FIG. 2. Sexual dimorphism. All matings.

TABLE I

DISTRIBUTION OF FREQUENCIES FOR FEMALES AND MALES IN THE UNSELECTED WHITE BAR POPULATION AND IN THE FORTIETH GENERATION OF LOW AND HIGH SELECTION FOR EYE FACET NUMBER

Each class has a range equal to ten per cent. of its mean.

Facets in Each Class	Classes in Factorial Units		Unselected Population		F40			
					Low		High	
	♀	♂	♀	♂	♀	♂	♀	♂
359–396.......	+19.07	+12.95						
325–358.......	+18.07	+11.95						
294–324.......	+17.07	+10.95		1				
266–293.......	+16.07	+ 9.95	1					
241–265.......	+15.07	+ 8.95		3				2
218–240.......	+14.07	+ 7.95		6				5
197–217.......	+13.07	+ 6.95		15				17
178–196.......	+12.07	+ 5.95		16			1	20
161–177.......	+11.07	+ 4.95		26			8	21
146–160.......	+10.07	+ 3.95		19			12	14
132–145.......	+ 9.07	+ 2.95	1	34			23	20
119–131.......	+ 8.07	+ 1.95		35			12	2
108–118.......	+ 7.07	+ 0.95	7	33			9	2
98–107.......	+ 6.07	− 0.05	11	50			4	
89–97	+ 5.07	− 1.05	27	55				
81–88	+ 4.07	− 2.05	25	37				
73–80	+ 3.05	− 3.05	29	29				
66–72	+ 2.07	− 4.05	51	23				
60–65	+ 1.07	− 5.05	55	22				
54–59	+ 0.07	− 6.05	54	18	1	7		
49–53	− 0.93	− 7.05	58	8	8	3		
44–48	− 1.93	− 8.05	54	7	19	34		
40–43	− 2.93	− 9.05	47	2	33	24		
36–39	− 3.93	−10.05	40	1	21	9		
33–35	− 4.93	−11.05	15	1	2			
30–32	− 5.93	−12.05	9		1			
27–29	− 6.93	−13.05	3					
24–26	− 7.93	−14.05	1					
22–23	− 8.93	−15.05						
20–21	− 9.93	−16.05	1					
Totals......			489	441	85	77	69	104

basis of the present selection series, and of the fortieth generation of low and of high selection for eye facet number. The column at the extreme left gives the facet values of the classes. The second and third columns give the factorial values of these classes, a unit of value being a difference in germinal or environmental factors which produces a ten per cent. change in facet value. The mean values of the unselected population are taken as zero and in the second column there are given the values on this scale for the females and in the third column for the

males. It will be noticed that there is considerable variation in both females and males, but the mean values as represented by the figures in heavy type are a consider-

TABLE II

SEXUAL DIMORPHISM. DIRECT LINE

Sexual dimorphism for each of the 42 generations of selection for low and high facet number. All values are in ten per cent. factorial units. Such a unit is any difference in germinal or environmental factors which produces a ten per cent. change in facet number.

Generation	Low Line		High Line		Difference in Dimorphism Between High and Low Lines
	Dimorphism	Total Change in Dimorphism	Dimorphism	Total Change in Dimorphism	
P.....	6.12	0.00	6.12	0.00	0.00
1.....	3.34	−2.78	2.74	−3.38	−9.60
2.....	2.25	−3.87	2.36	−3.76	0.11
3.....	0.95	−5.17	1.54	−4.58	0.59
4.....	1.12	−5.00	1.61	−4.51	0.49
5.....	2.20	−3.92	4.89	−1.23	2.69
6.....	2.61	−3.51	2.13	−3.99	−0.48
7.....	3.26	−2.86	3.82	−2.30	0.56
8.....	0.92	−5.20	4.17	−1.95	3.25
9.....	0.69	−5.43	4.74	−1.38	4.05
10.....	0.48	−5.64	4.17	−1.95	3.69
11.....	2.17	−3.95	3.38	−2.74	1.21
12.....	1.49	−4.63	5.28	−0.84	3.79
13.....	1.20	−4.92	3.20	−2.92	2.00
14.....	1.67	−4.45	3.22	−2.90	1.55
15.....	1.26	−4.86	2.41	−3.71	1.15
16.....	0.21	−5.91	2.16	−3.96	1.95
17.....	1.13	−4.99	3.33	−2.79	2.20
18.....	1.51	−4.61	4.29	−1.83	2.78
19.....	0.78	−5.34	2.31	−3.81	1.53
20.....	0.55	−5.57	2.45	−3.67	1.90
21.....	0.59	−5.53	3.58	−2.54	2.99
22.....	1.08	−5.04	0.79	−5.33	−0.29
23.....	1.38	−4.74	——	——	——
24.....	3.17	−2.95	1.87	−4.25	−1.30
25.....	1.05	−5.07	2.18	−3.94	1.13
26.....	0.61	−5.51	0.57	−5.55	−0.04
27.....	1.14	−5.98	2.19	−3.93	1.05
28.....	1.35	−4.77	1.24	−4.88	−0.11
29.....	0.75	−5.37	1.46	−4.66	0.71
30.....	1.04	−5.08	1.40	−4.72	0.36
31.....	1.07	−5.05	2.29	−3.83	1.22
32.....	1.01	−5.11	1.46	−4.66	0.45
33.....	1.97	−4.15	2.09	−4.03	0.12
34.....	1.03	−5.09	2.67	−3.45	1.64
35.....	2.75	−3.37	4.11	−2.01	1.36
36.....	0.83	−5.29	3.22	−2.90	2.39
37.....	2.10	−4.02	2.13	−3.99	0.03
38.....	0.71	−5.41	1.79	−4.33	1.08
39.....	2.53	−3.59	2.08	−4.04	−0.45
40.....	0.26	−5.86	2.20	−3.92	1.94
41.....	0.95	−5.17	1.93	−4.19	0.98
42.....	1.37	−4.75	3.24	−2.88	1.87

able distance apart, six class units or, to be more exact, 6.12 as stated in the first paragraph. In both low and high selection lines it is to be noticed that the variability has decreased and at the same time the mean values of females and males have approached each other. This approach is greater in the low than in the high line.

Tables II and III give the sexual dimorphism for the parental unselected generation and for each of the 42 generations of selection. Each table includes, for both low and high lines, the value of the dimorphism for each generation and the decrease since the beginning of selection. In the last column of each table there is a comparison of the dimorphisms in the two selection lines. Table II includes only the offspring in the direct line. Table III gives the data for the same series, but includes sib matings as well as those in the direct line.

Figures 1 and 2 show the decrease in graphic form. The vertical scale is in factorial units as described above. The upper horizontal line is at the level of the dimorphism value of the unselected population, which is 6.12 units in favor of the males. The lower horizontal line indicates the position of zero difference between the sexes. The scale at the left gives the actual dimorphism values and the scale at the right the departures from the original value. The continuous zigzag line gives the values for each generation in the low selection series and the dotted line those in the high selection series. Special emphasis is to be laid on the fact that selection was not for low or high sexual dimorphism, but for low or high facet number regardless of dimorphism. In no sense can it be considered as a direct selection for degree of dimorphism.

The result obtained when the offspring of all matings are taken (Fig. 2) is not essentially different from that obtained in the direct line. Since it gives the smoother curve because of the larger number of individuals it will be used as the basis of the following discussion.

In the low selection line the dimorphism drops very

rapidly from its original value of 6.12 units to 1.12 in the fourth generation. From that point on it shows some increase and fluctuates irregularly for a number of gen-

TABLE III

SEXUAL DIMORPHISM. ALL MATINGS

Sexual dimorphism for each of the 42 generations of selection for low and high facet number. All values are in ten per cent. factorial units. Such a unit is any difference in germinal or environmental factors which produces a ten per cent. change in facet number.

Generation	Low Line		High Line		Difference in Dimorphism between High and Low Lines
	Dimorphism	Total Change in Dimorphism	Dimorphism	Total Change in Dimorphism	
P.....	6.12	0.00	6.12	0.00	0.00
1.....	3.34	−2.78	2.76	−3.36	−0.58
2.....	1.95	−4.17	1.78	−4.34	−0.17
3.....	1.63	−4.49	1.45	−4.67	−0.18
4.....	1.12	−5.00	1.72	−4.40	0.60
5.....	2.20	−3.92	3.47	−2.65	1.27
6.....	2.06	−4.06	2.44	−3.68	0.38
7.....	3.36	−2.76	3.70	−2.42	0.34
8.....	0.84	−5.28	3.87	−2.25	3.03
9.....	0.68	−5.44	3.35	−2.77	2.67
10.....	0.98	−5.14	3.64	−2.48	2.66
11.....	1.99	−4.13	3.29	−2.83	1.30
12.....	1.28	−4.84	4.74	−1.38	3.46
13.....	1.88	−4.24	3.20	−2.92	1.32
14.....	0.43	−5.69	3.42	−2.70	2.99
15.....	1.42	−4.70	2.44	−3.68	1.02
16.....	0.31	−5.81	2.80	−3.32	2.49
17.....	0.61	−5.51	3.19	−2.93	2.58
18.....	1.07	−5.05	4.29	−1.83	3.22
19.....	0.81	−5.31	2.31	−3.81	1.50
20.....	0.33	−5.79	2.66	−3.46	2.33
21.....	0.33	−5.79	3.70	−2.42	3.37
22.....	0.92	−5.20	3.72	−2.40	2.80
23.....	1.42	−4.70	3.33	−2.79	1.91
24.....	2.23	−3.89	2.97	−3.15	0.74
25.....	0.83	−5.29	2.71	−3.41	1.88
26.....	1.26	−4.86	1.71	−4.41	0.45
27.....	0.75	−5.37	2.15	−3.97	1.40
28.....	1.30	−4.82	1.07	−5.05	−0.23
29.....	0.94	−5.18	1.22	−4.90	0.28
30.....	0.89	−5.23	1.32	−4.80	0.43
31.....	1.23	−4.89	1.79	−4.33	0.56
32.....	0.69	−5.43	1.60	−4.52	0.91
33.....	1.55	−4.57	1.78	−4.34	0.23
34.....	1.00	−5.12	2.51	−3.61	1.51
35.....	1.84	−4.28	2.68	−3.44	0.84
36.....	0.86	−5.26	2.58	−3.54	1.72
37.....	1.61	−4.51	2.44	−3.68	0.83
38.....	0.71	−5.41	2.01	−4.11	1.31
39.....	1.75	−4.37	2.03	−4.09	0.28
40.....	0.56	−5.56	2.32	−3.80	1.76
41.....	0.77	−5.35	1.90	−4.22	1.13
42.....	1.37	−4.75	3.24	−2.88	1.87

erations, but eventually settles down to a value not far from 1.00. This last value may therefore be taken as the normal dimorphism in a homozygous low bar population.

In the high selection line there is a similar rapid decline, in this case from 6.12 in the parental generation to 1.45 in the third selection generation. There is then a pronounced increase and fluctuation between 2.00 and 4.00 from the fifth to the twenty-third generation. After a second general decline the value remains for most of the time between 1.00 and 2.50.

While the general course of the curves is the same in the two cases, the low selection line is the more consistent and reaches the lower level.

The probable explanation of the decrease in dimorphism in both selection lines is to be sought in the fact that some of the accessory factors affecting facet number are sex-linked. The unselected population is a mixed one and accordingly has a considerable degree of heterozygosis for these factors in the females. One of the results of selection for facet number with inbreeding is a decrease in this heterozygosis, leaving the females homozygous for low facet factors in the low line and for high facet factors in the high line. As long as the population is homozygous it is probable that the degree of dimorphism does not change to any great extent because there is no disturbance of the factorial proportions. An increase on one side is accompanied by a proportionate increase on the other. The same would be true as far as the heterozygous females are concerned if the dominance of low and high factors were alike. If, however, the factors for low facet number have a higher dominance coefficient than those for high facet number it follows that selection as practised will produce a decrease in dimorphism. That this will be true in both low and high lines is made clear by the consideration that heterozygous females under the stated condition must be lower than the average of the homozygous ones in the same population. When these heterozygotes are eliminated

by selection it follows that the mean value of the females approaches that of the males.

The explanation for the general decrease seems clear enough, but the reasons for some of the details are not so evident. The dimorphism in the high selection line is higher than that in the low selection line in nearly every generation. In part this difference may be due to a faulty method of determination of the dimorphism value. If degree of dimorphism were expressed in facet numbers the high line would of course have a much greater difference between the sexes than the low line. The factorial unit method with its logarithmic scale based primarily upon the observed effects of temperature is undoubtedly a much better one than that based upon the unreduced facet numbers, though a simple ratio between the facet numbers of the two sexes might have served equally well in the present case.[3] But the correction is only an approximation and may not be great enough to obtain the most rational value.

In part, however, the difference between the two lines may be due to the greater frequency of appearance of mutant accessory factors in the high than in the low line. Such factors introduce a new heterozygosis and therefore increased dimorphism which is eliminated only by later selection. That such mutants appear is evidenced by increase in standard deviation.

The appearance of mutants and their prompt elimination by selection may account also for some of the irregular fluctuations as observed in both lines. It is possible, however, that environmental factors may exercise a differential effect and thereby change the dimorphism. In favor of this view it may be pointed out that there is some tendency for the values in the low and high lines to fluctuate together and this may be explained by the fact that the food cultures of the two lines in any generation were usually made up from the same food mass.

[3] Zeleny, C., 1920, "The Tabulation of Factorial Values," Amer. Nat., 54: 358–362.